Population Structure of the Freshwater Crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney Region, Australia

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The structures of *Euastacus spinifer* populations in two pools of the Loddon River (south of Sydney, New South Wales) are described. No significant differences in catchabilities have been detected between the sexes, related to size classes, or between precocious (very small, sexually mature males) and normal males. Sex ratios in both populations show similar long-term trends, although short-term fluctuations are evident. Normal males comprise about 50% of populations up to 25–30mm CL, but above this size the male percentage declines well below 50%. Substantial rises and declines in frequencies of precocious males are noted, although few survive above 30mm CL; however, generally there is a surplus of males in the Loddon populations.

Frequency distributions are skewed to the smallest size classes, with pulses of recruitment detected in spring and summer; numbers of mature adults captured are low, females (3%) and males (6%) from Pool 3. It is suggested that the dominance of smaller size groups at Loddon River sites may be related to lowered predation, especially by eels.

Possible origins of the precocious males are discussed and two hypotheses advanced to explain their observed abundances relative to females; however, the available data do not permit a decision between almost total mortality over a confined size range (25–30mm CL) or recent selective recruitment of precocious males to the study populations.

INTRODUCTION

Although a number of studies have been published on stocked or intensively managed populations of commercial crayfishes (Huner 1978; Keller 1993; Morrissy 1979), relatively few detailed sampling programs have been completed on wild populations of non-commercial species. But several general findings are relevant here. Firstly, cray populations comprise a large proportion of the biomass in many aquatic systems; up to 30% in a stream ecosystem has been reported with standing crop estimates of 1345 kg/ha/year (Hogger 1988).

Secondly, the holding capacity of a habitat is more important in controlling population size than pressures such as predation. The two major factors determining holding capacity are the availability of suitable habitat (presence of suitable cover or hides) and the relative abundance of food (Hogger 1988). An impoundment may support a population many times larger than an adjacent lotic waterway and this population may have totally different characteristics, due to modified selection pressures (Hogger 1988). It has also been demonstrated that, although found in a variety of environments, even closely

related species have distinct flow and depth or substrate preferences (Eversole and Foltz 1993; Hogger 1988).

Thirdly, although males often dominate the largest size classes (Honan and Mitchell 1995a), long-lived species have higher mortality in early life stages when growth is most rapid (Momot and Hauta 1995). Finally, maturing males may regulate the growth and mortality rates in other individuals, so restricting the recruitment of juveniles (Momot 1993).

Population studies have been done on a few species in other Australian genera (Hamr 1990; Hamr and Richardson 1994) but, with the exception of recent studies on three Victorian species nothing has been published on *Euastacus*. Barker (1992) reported preliminary surveys of *Euastacus armatus, E. bispinosus* and *E. kershawi*, while Honan and Mitchell (1995a,b) focused more detailed investigations on *E. bispinosus*.

Catchability, Sex Ratios and Population Density.

Catchability varies due to a number of factors. Aside from trap design and density, individual differences in mobility (related to sex or size), behaviour (related to moult or reproductive phase) or distribution (related to preferred habitat and food resources) influence catches (Hogger 1988).

In *E. bispinosus* catchability varied seasonally. This species exhibited most activity in winter, with mature females dominating catches during the winter brooding season (May - November). In summer catch rates were low and male juveniles dominated the samples (Honan and Mitchell 1995a).

Variations in sex ratios with size are widespread among crustaceans, although apart from well-documented instances of sequential hermaphroditism, the origins of these variations are generally unknown (Wenner 1972). But recently social control of growth, particularly inhibition of growth in small individuals, has been demonstrated in another decapod (Karplus et al. 1991, 1992). For most freshwater crays the observed sex ratio changes during the year. In the breeding season adult males are usually caught more frequently, but at other times the ratio reverts to 1:1 (Honan and Mitchell 1995a).

Although previously not reported in parastacids, a separate sub-group of very small but sexually mature males has been detected in some *E. spinifer* populations (Morgan 1997; Turvey and Merrick 1997a). These individuals, characterised by highly inflated genital papillae and high gonosomatic indices, have been designated precocious males; sizes at maturity of female, normal male and precocious male *E. spinifer* are documented in Turvey and Merrick (1997a).

Extreme fluctuations of crayfish numbers in local areas have been recorded and density is known to influence growth rates, reproductive capacity, age at maturity and life-span within a population (Hogger 1988). The density of the *E. bispinosus* population, at one site, was estimated to be one large (>85mm CL) individual for every 2–5m of bank, although many other smaller individuals were also present. The majority of these crays had a home range of less than 75m (Honan and Mitchell 1995a).

The objectives of this paper are: to infer relative abundances in populations of females as well as normal and precocious males of different sizes, from their abundances in catches (on the basis of equal average catchability); to document trends in the structures of cray populations in the study areas, particularly with respect to the occurrence of precocious males; to present two hypotheses to account for the observed abundances.

MATERIALS AND METHODS

Major features of the Loddon River site (lat. 34°17′S: long. 150°54′E) are documented in Turvey and Merrick (1997a), but more details of sampling techniques and marking methods follow. Sampling was conducted at approximately monthly intervals,

during the last quarter and new moon phases of the lunar cycle, when the moon was not visible in the night sky; netting commenced one or two hours after dark and continued for five hours. Net stations were permanently marked with pegs at regular intervals along the length of each pool (every 6m for Pool 3, every 5m for Pool 7). The number of nets deployed at each station was proportional to the width of the pool at that point; at each session nets were placed in the same positions, in a rectangular grid pattern.

The 40 nets set in Pool 3 (54m long, ~770m^2) and 22 nets in Pool 7 (40m long, ~320m^2) were hauled, checked and returned to original positions every 30 minutes. Captured specimens were immediately placed in wet hessian bags until relevant catch data (e.g. time, net station, carapace length (CL), sex, condition) were recorded prior to marking and/or release; all captives were returned to the part of the pool from which they came. Individuals were marked by removing distal portions of the abdominal pleura and tail fan using scissors or a leather punch; these marks were clearly visible after at least one moult (Fig. 1).

Average Catchability

Average catchabilities were estimated from monthly catches (Pools 3, 7) during the mark-recapture study. From mark-recapture records, individuals were considered available for capture during a particular period if they were captured on or before the first sampling, and on or after the last sampling of the period. Proportions of actual captures among total opportunities were used to estimate average catchabilities in selected sex and size groups. Estimates were determined separately for females and normal males in four carapace length classes from Pool 3, and two CL classes from Pool 7, for the periods November 1977-February 1978 and May-August 1978 (Table 1); results for each period and pool were analysed separately.

Initially, average catchabilities of normal males and females within each class were tested for significant differences using chi-squared values calculated from contingency tables; the difference between overall catchabilities (combined for size classes) of males and females was similarly tested. The relationship between catchabilities of males and females was tested for heterogeneity among size classes. An additional comparison between the catchabilities of large males and females (75–100mm CL) was also conducted for the period February-May 1978.

Average catchabilities were recalculated for the combined data (normal males, females) in each size class where, for a particular period and location, there were no significant results in the preceding analysis. Combined average catchabilities of normal males and females were tested for heterogeneity with respect to size class, separately for each period and location, using a variance test for homogeneity of the binominal distribution (Snedecor and Cochran 1967). Average catchabilities of large females (75–100mm CL) from Pool 3 were also included in this analysis. When this overall test indicated significant differences among catchabilities in different size classes, the class with the most obviously different value was removed and the test recalculated.

An attempt was also made to compare catchabilities of precocious and normal immature males; this test was confined to individuals of 20–25mm CL. Data for three sampling periods (12 months, July 1977–June 1978) were combined. To eliminate bias, random samples of normal males were selected so that ratios of normal to precocious males were fixed for each location. Combined data were then used to test for significant differences between precocious and normal males for each of the two locations, using 2 x 2 contingency tables.

Sex Ratios

Catches were initially analysed for changes in relative abundances of females and males of different sizes over the duration of the mark-recapture study. Both sexes were allocated to five length classes (20–30mm, 30–40mm, 40–50mm, 50–70mm, 70–100mm CL);
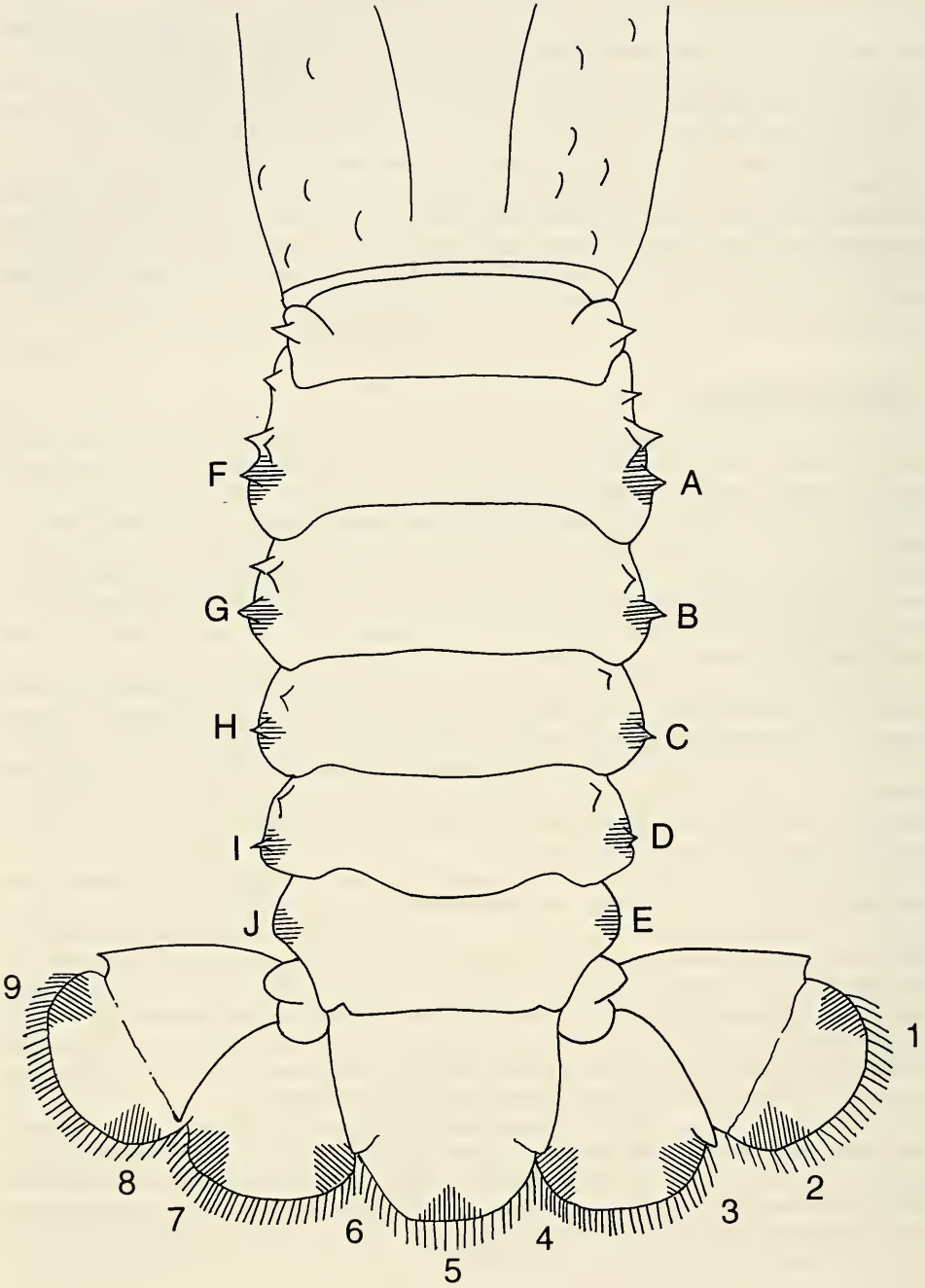
Figure 1. Dorsal view of an *E. spinifer* abdomen with uropods extended. The identification for each individual consisted of a single pleural mark combined with up to four tail fan markings; shaded areas denote the sections removed (e.g. A 13 to I 4679).

separate distributions of percentage of catch with month were constructed for each sex and size class at each location. Differences between the distributions were tested for significance using a Kolmogorov-Smirnov test (Siegel 1956).

To investigate fluctuations, over time, in numbers of normal and precocious males the two groups were allocated to four classes (<20mm, 20–25mm, 25–30mm, 30–35mm CL) at both locations. Total catches of males less than 35mm (CL) were tabulated for the periods May-August 1977, September-December 1977, January-April 1978, May-August 1978, and September-December 1978. The percentage of each catch attributable to precocious or normal males in each class was calculated and percentages plotted as frequency histograms for each period (Fig. 3).

Average sex ratios of crayfish populations in Pools 3 and 7 were determined for the total study period, and interpreted on the basis of catchabilities and variation over time in relative abundances of females, normal and precocious males. The total catch from each location was divided into five classes (from 10mm CL). Percentage frequencies of normal and precocious males (in the total catch for each size class) were calculated, and relationships between frequencies and carapace lengths constructed for both locations. Confidence limits (95%) for mean frequencies with repeated sampling were also plotted, based on tables by Crow (1956) for small sample sizes (≤30), or on a normal approximation for samples of larger size (Snedecor and Cochran 1967). This procedure was also applied to combined catches (June, July, August, and November 1976 from Pool 7) as well as several catches from two other pools.

Size Frequency Classes

Monthly catches from the mark-recapture study were combined for the periods May-August 1977, September-December 1977, January-April 1978, May-August 1978, and September-December 1978, for each sampling location. Size (CL) frequency histograms were constructed for crays in each combined catch (Fig. 6) and changes, over time, in the size structure of catches were noted for both populations.

RESULTS

Average Catchability

There were no significant differences (p >0.05) in the average catchabilities of males or females for the periods of testing, either within any size class, or when classes were combined to provide overall estimates (Table 1); furthermore, there were no instances of significant heterogeneity (p >0.05) among size classes in the relationships between catchabilities of males and females.

When average catchabilities were combined for each sex and tested for homogeneity with respect to size, there was significant heterogeneity for both periods in Pool 3 (Table 2). Removal of the 75–100mm size class from the November 1977–February 1978 series rendered the catchabilities of remaining classes homogeneous (p >0.25); similar results were obtained for May-August 1978 by removing the 30–40 mm class (p >0.50). Catchabilities of each of these classes were aberrant in only one of the two periods. There was no significant heterogeneity (p >0.05) with respect to size in the catchabilities of crays from Pool 7 for either period.

By contrast, there was an apparent difference between observed and expected catches of precocious and normal males from Pool 3 for the period November 1977–February 1978 (Table 3). But separate testing, using a 2 x 2 contingency table, did not confirm this (X^2 corrected for continuity = 1.42, d.f. = 1, 0.25> p >0.1); the observed and expected catches were extremely close for all other periods, for both locations. On

this basis, the data for the three periods were combined for each location, and no significant differences were detected between the catchabilities of precocious and normal males.

TABLE 1

Comparisons of average catchabilities of female and normal male *E. spinifer*.

Location & Period	Size Class (mm)	Female		Male		χ^2 (1 d.f.)	p
		*P	N	P	N		
Pool 3:	20–30	0.48	104	0.50	104	0.08	>0.25
Nov. 1977–Feb. 1978	30–40	0.31	32	0.42	36	0.79	>0.25
	40–50	0.55	40	0.34	44	3.70	>0.05
	50–75	0.39	36	0.47	32	0.44	>0.50
	Overall	0.45	212	0.45	216	0.01	>0.90
	Heterogeneity χ^2 = 5.02 (3 d.f.)						>0.10
Pool 3:	20–30	0.21	52	0.15	40	0.57	>0.25
May 1978–Aug. 1978	30–40	0.41	132	0.37	112	0.47	>0.25
	40–50	0.18	28	0.13	16	0.22	>0.50
	50–75	0.29	24	0.22	32	0.39	>0.50
	Overall	0.33	236	0.28	200	1.10	>0.25
	Heterogeneity χ^2 = 0.55 (3 d.f.)						>0.90
Pool 7:	20–40	0.18	44	0.14	56	0.28	>0.50
Nov. 1977–Feb. 1978	40–70	0.18	76	0.25	16	0.36	>0.50
	Overall	0.18	120	0.17	72	0.09	>0.50
	Heterogeneity χ^2 = 0.56 (1 d.f.)						>0.25
Pool 7:	20–40	0.61	64	0.57	44	0.18	>0.50
May 1978–Aug. 1978	40–70	0.41	68	0.63	16	2.38	>0.10
	Overall	0.51	132	0.58	60	0.95	>0.25
	Heterogeneity χ^2 = 1.61 (1 d.f.)						>0.10
Pool 3:	75–100	0.14	36	0.08	12	0.25	>0.50
Feb. 1978–May 1978							

*P is the proportion of captures among the total number of opportunities for capture (N) of crayfishes known to be present during the given period.

Sex Ratios

Female and male *E. spinifer* in both locations showed similar overall trends in capture frequency during the mark-recapture study (Fig. 2), although short-term differences were evident. The only evidence of a change through time in the relative capture frequencies of males and females was for crays in the 20–30mm CL class in Pool 7 (Table 4). In this instance the difference between males and females just failed to reach the 5% level of significance (D = 0.168, critical 5% value of D = 0.171), suggesting a trend towards an increasing number of males relative to females in the later part of the study.

Size frequency distributions of precocious and normal males (Fig. 3) indicated that, in Pool 7, there was a substantial increase in precocious male numbers relative to normal

males in the 20–25mm class, during the period May 1977–April 1978. This increase was concomitant with rises in relative numbers of smaller, normal males, and was followed by a sharp increase in relative numbers of precocious males in the 25–30mm class from May-August 1978. Relative numbers of both groups were approximately equal, during September-December 1978, at all sizes except the 30–35mm class from which precocious males were absent. Relative numbers of precocious males also increased in Pool 3 over the same period. Normal males were initially more abundant in the 20–25mm and 25–30mm classes, while approximately equal numbers of precocious and normal males were present in the 30–35mm group. By the end of the mark-recapture study numbers of precocious and normal males were approximately equal, except in the 30–35mm class in which normal males were more abundant. Relative abundances of precocious and normal males also differed considerably between periods twelve months apart at both locations.

TABLE 2

Comparisons of average catchabilities of *E. spinifer* in different size classes — combined for females and normal males.

| Location | Size Class | PERIOD | | | |
| | | Nov 1977–Feb 1978 | | May 1978–Aug 1978 | |
		*P	N	P	N
Pool 3	20–30	0.49	208	0.18	92
	30–40	0.37	68	0.39	244
	40–50	0.44	84	0.16	44
	50–75	0.43	68	0.25	56
	†75–100	0.18	28	0.19	36
	Overall	0.43	456	0.30	472
		Overall Homogeneity		Overall Homogeneity	
		‡$\chi^2_c = 11.4$, d.f. = 4		$\chi^2 = 21.9$, d.f. = 4	
		0.025> p >0.01		p <0.005	
		Minus 75–100		Minus 30–40	
	Adjusted	0.45	428	0.20	228
		Remaining Homogeneity		Remaining Homogeneity	
		$\chi^2_c = 3.4$, d.f. = 3		$\chi^2 = 1.5$, d.f. = 3	
		p >0.25		p >0.50	
Pool 7	20–40	0.16	100	0.59	108
	40–70	0.20	92	0.45	84
	Overall	0.18	192	0.53	192
		Overall Homogeneity		Overall Homogeneity	
		$\chi^2_c = 0.21$, d.f. = 1		$\chi^2 = 3.19$, d.f. = 1	
		p > 0.50		0.1 > p > 0.05	

*P is the proportion of captures among the total number of opportunities for capture (N) of crays known to be present during the given period.
†Females only.
‡Chi-squared corrected for continuity.

TABLE 3

Comparisons of average catchabilities of precocious and normal male *E. spinifer* with carapace lengths of 20–25 mm.

Male Type	SEPARATE PERIODS								
	Jul–Oct 1977			Nov 1977–Feb 1978			Mar–June 1978		
	*C	E	N	C	E	N	C	E	N
				Location — Pool 3					
Precocious	1	1	4	7	4.8	12	3	2.5	8
Normal	3	3	12	12	14.2	36	7	7.5	24
				Location — Pool 7					
Precocious	6	5	16	3	4	16	1	1.5	8
Normal	4	5	16	5	4	16	2	1.5	8

Location	COMBINED PERIODS					
	Precocious		Normal		χ^2_e	p
	P	N	P	N	(1d.f.).	
Pool 3	0.46	24	0.31	72	1.23	>0.25
Pool 7	0.25	40	0.28	40	0	~1

* C is the observed number of captures among the total number of opportunities for capture (N) of crays known to be present during the given period. E is the expected value for C under the null hypothesis that there is no difference between the frequency of capture of precocious and normal males that are known to be present. As in previous tables, P = C/N.

TABLE 4

Summary of Kolmogorov-Smirnov Tests results comparing trends through time in the capture frequencies of male and female *E. spinifer*.

Size Class	Pool 3				Pool 7			
	F	M	D	p	F	M	D	p
20–30	259	224	11	>0.1	116	140	17	≈0.05
30–40	271	209	11	>0.1	136	67	12	>0.1
40–50	81	78	19	>0.1	24	24	17	>>0.05
50–70	48	74	23	>0.1	117	45	11	>0.1
70–100	28	28	39	>>0.05	17	17	24	>>0.05

F = total catch of females.
M = total catch of males.
D = maximum difference between the cumulative distributions of percent frequency of capture vs. month for males and females.
p = the probability of obtaining a difference equal to or greater than the observed difference D purely by chance, given that the two distributions were from the same population.

Abundances in catches of males, relative to females, varied among the different size classes in Pools 3 and 7 (Fig. 4). In Pool 3, approximately 50% of individuals less than 25mm CL were male, while the 50% occurrence of males extended to 25–30mm CL in Pool 7. At all locations except Pool 3 (Figs. 4 and 5) there was a trend for the percentage of males to remain below 50% among crays greater than 30mm CL. There was evidence of fluctuations (with CL) in percentages of males in these larger classes, but both cyclic percentage changes and irregular variations were within limits of error inherent with the small samples of many size classes.
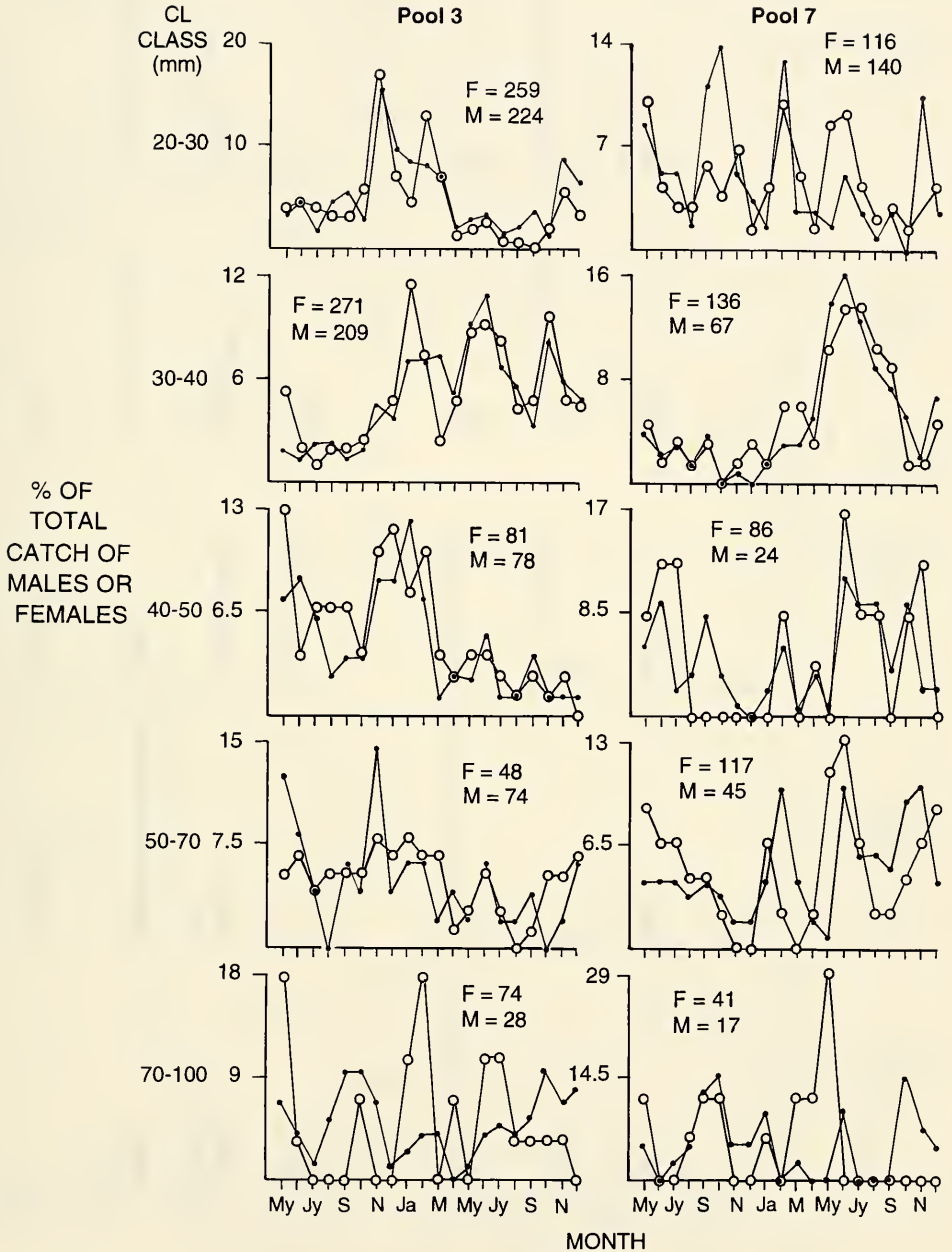
Figure 2. Changes over the mark-recapture study in capture frequencies of *E. spinifer* from two Loddon River pools. Total catches of females and males are included in each graph. Key to symbols: ● = females; ○ = males; ◉ = both sexes combined.
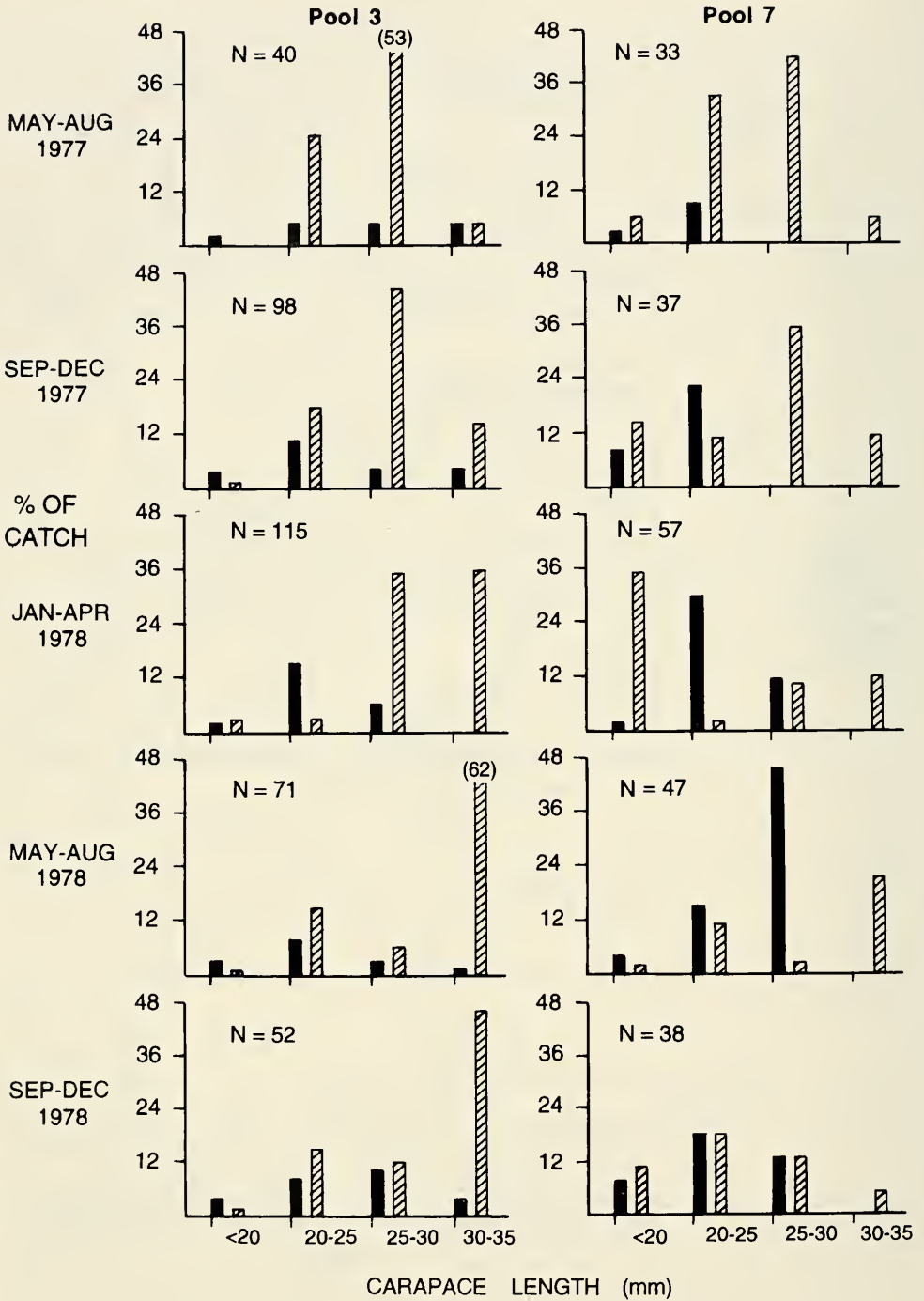
Figure 3. Changes over the mark-recapture study in relative capture frequencies of precocious and normal male *E. spinifer* in the smaller size classes. The total catch of males in all of the included size classes (N) is listed in each graph. Key to symbols: ■ = precocious males; ▨ = normal males.
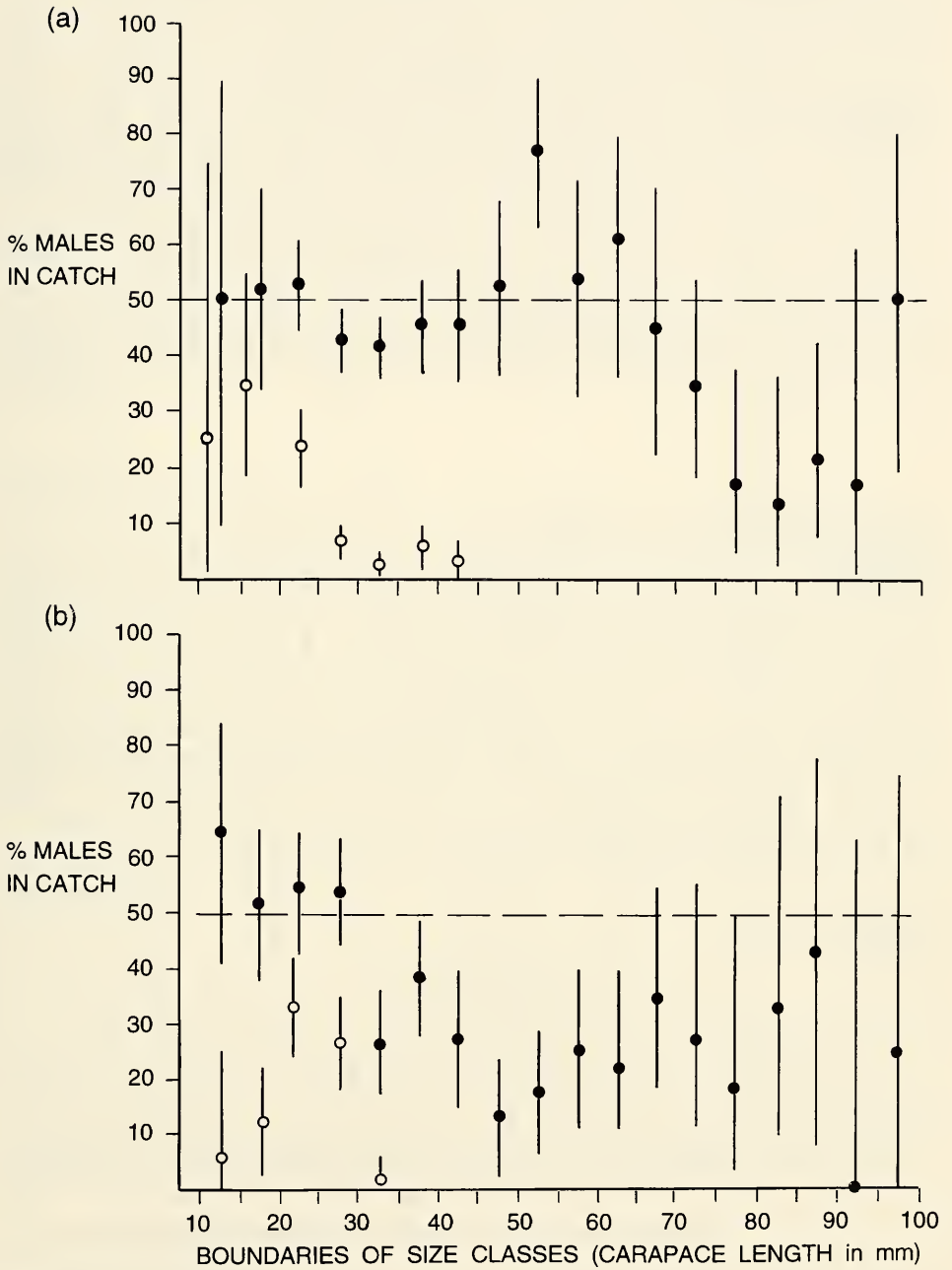
Figure 4. Changes with carapace length in the frequency of capture of male *E. spinifer* relative to females, averaged over the mark-recapture study: (a) Pool 3; (b) Pool 7. Key to symbols: ● = normal males; ○ = precocious males; | = 95% confidence limits for the mean percentage on repeated sampling.
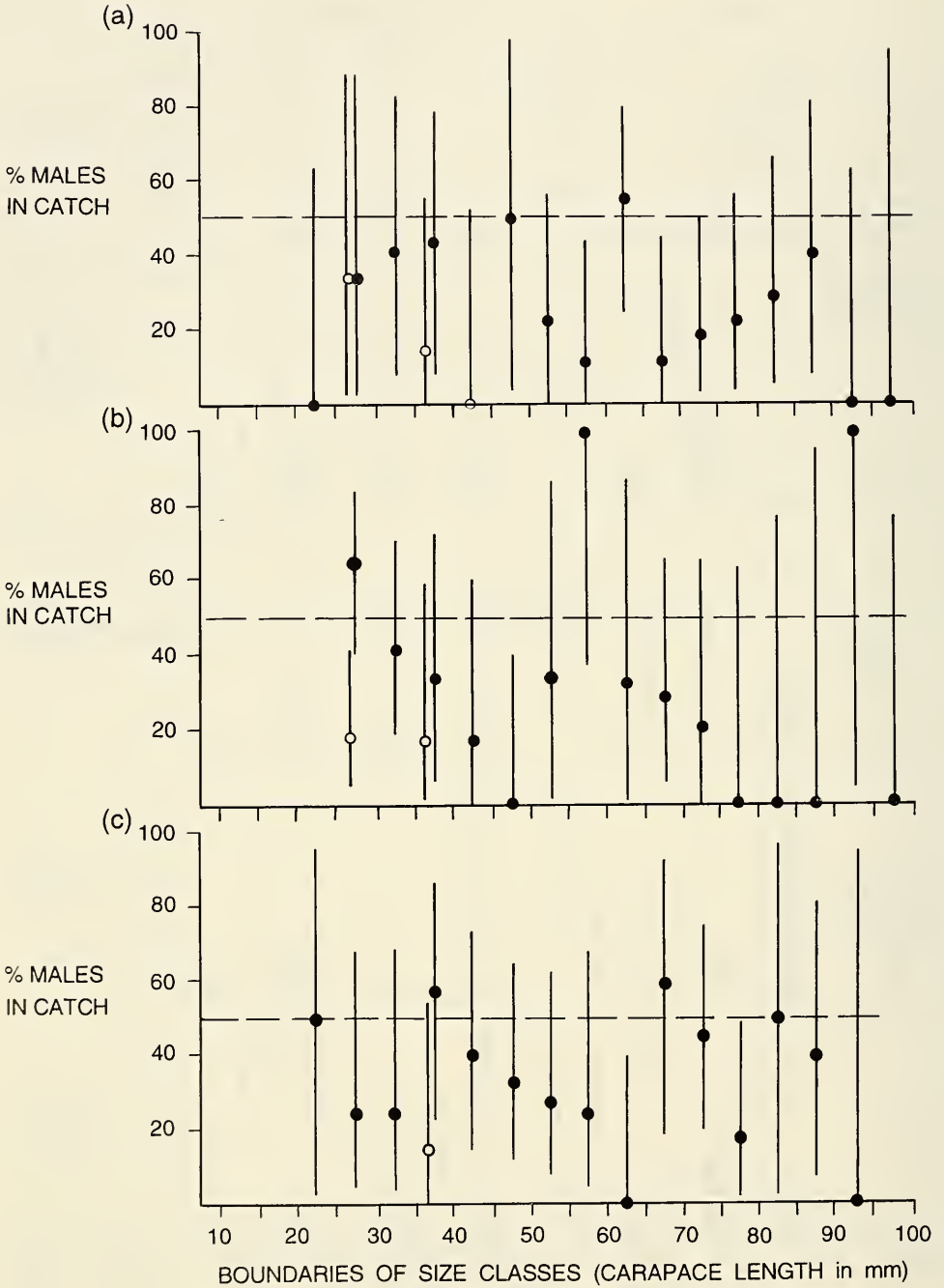
Figure 5. Changes with carapace length in the frequency of capture of male *E. spinifer* relative to females for catches taken in three Loddon River pools: (a) Pool 7, catches during June, July, August and November 1976; (b) Pool 6, catches during December 1977; (c) Pool 8, catches during January and June 1978. Key to symbols: ● = normal males; ○ = precocious males; | = 95% confidence limits for the mean percentage on repeated sampling.

In Pool 3 (Fig. 4a), the percentage of males was significantly less than 50% (p <0.05) for individuals in both 25–30mm and 30–35mm CL classes. This reduced incidence was followed by an increase to a level significantly greater than 50% (p <0.05) for the 50–55mm class, above this size male occurrence declined to a level well below 50%. In this pool (Fig. 4a), precocious males comprised approximately 25% of catches of small individuals (<25mm CL), although these percentages may have been subject to considerable sampling error. Frequencies of precocious males declined rapidly at sizes above 25mm CL; they remained at a low level up into the 40–45mm class, but above that they were absent.

In Pool 7 (Fig. 4b) there was a significant frequency increase in precocious males from the 15–20mm to the 20–25mm class (p <0.05), while they were captured with equal frequency in the 20–25mm and 25–30mm size classes. The abundance of precocious males declined to a low level from the 25–30mm to the 30–35mm class, above that size they were absent from catches. In both Pools 3 and 7 the decrease in overall abundance of males occurred over the same narrow CL range as the decline in precocious male abundance, although the size ranges at which these events occurred were different for the two locations.

Size Frequency Classes

The frequency distributions of crays captured during the mark-recapture study were skewed towards the smaller size classes (Fig. 6) in both pools, although small individuals (<20mm CL) were only abundant in Pool 7 catches from January-April 1978. The relative capture frequency of the 20–30mm class increased substantially during the period September-December 1977; this size grouping constituted a modal group which progressed into the 30–40mm class by September-December 1978. There was evidence of a similar increase in relative numbers of the 20–30mm class from September-December 1978 in Pool 3, but not in Pool 7. Frequency distributions for May-August 1977 and September-December 1977, in Pool 3, were thus dominated by the 20–30mm class; the same periods one year later were dominated by the 30–40mm class. A similar dominance existed in the May-August catches from Pool 7, but there was no dominant class in September-December 1978 catches corresponding to the 20–30mm cohort of one year earlier.

Of the total number of different individuals captured in Pool 3 during the study, approximately 3% were mature females, 6% were normal mature males, and 9% were precocious males.

DISCUSSION

The sampling techniques were designed to maximise recapture frequency. Preliminary observations had indicated larger catches on moonless nights and nets were deployed at the highest possible densities. To minimise confounding influences, such as dominance behaviour and differential mobility, all captured individuals were retained until the completion of each sampling. Pools were selected for their degree of separation and on size that enabled the whole pool to be fished intensively over a single collection session.

Average Catchability

Overall catchabilities calculated for normal males and females, in Pools 3 and 7, indicated that the null hypothesis (no difference between catchabilities of sexes) should be accepted (at a low level of significance) for each period at each location. Available data provided no evidence of a difference in average catchabilities of males and females over 75mm CL; however, few values were available for males. The average catchability
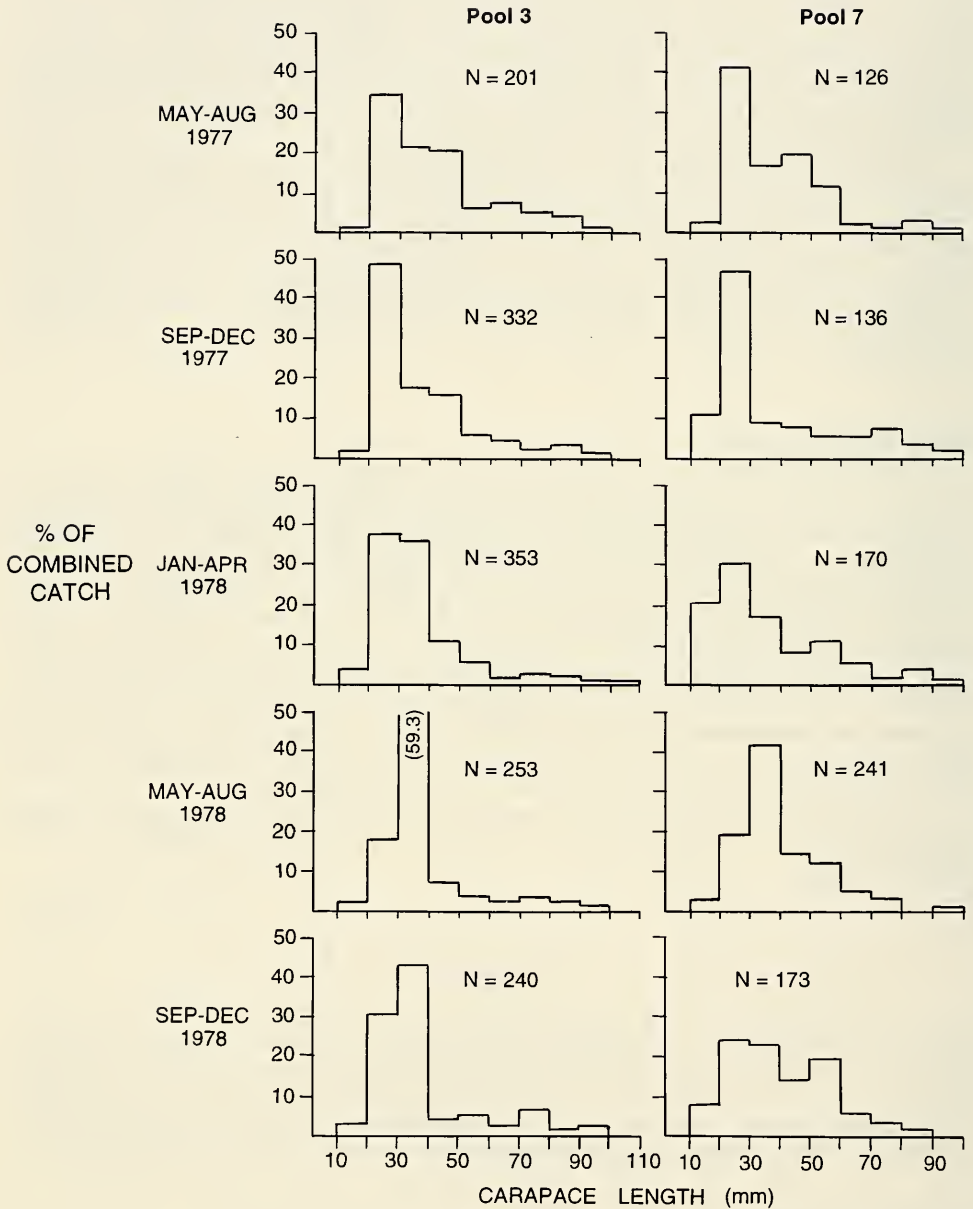
Figure 6. Size frequency distributions of *E. spinifer* captures taken over five periods during the mark-recapture study in Pools 3 and 7 (Loddon River). N = total number of captures for the period; percentage extending off graph is included in parentheses.

of these large females was also similar to that of both sexes in several smaller size classes, during the period May-August 1978. Taking these findings together there is no indication of any difference in catchability between large (>75mm CL) individuals and smaller size classes. The catchability comparison of precocious and normal juvenile males was restricted to a narrow size range, due to the virtual absence of multiple recapture records for precocious males of other carapace lengths. Data for the three sampling periods (July-October 1977; November 1977–February 1978: March-June 1978) were combined because precocious samples were insufficient to test for heterogeneity between periods. There was no evidence that catchability of precocious males differed from that of normal males of similar size when data were combined for 12 month periods. This finding, together with the similarity of actual and expected catches for most shorter sampling periods, suggests that catchabilities of precocious and normal males do not differ.

Extension of this conclusion to the entire *E. spinifer* population throughout the study area cannot be definite; however, the results for most females and normal males for eight months of a year in two pools, precocious male data and the probability that large individuals conformed to patterns for smaller size groups all support the concept of equal average catchabilities within size classes.

Sex Ratios

As capture frequencies for males and females, within different size classes, did not differ over the duration of the study (Fig. 2 and Table 4) relative abundances were estimated by calculating the percentage frequency of males in the total catch (for each size class) over the entire period. These estimations indicated that, in Pool 7, the percentage of males was well below 50% in the range 30–100mm CL (Fig. 4b). Similar results were obtained for Pool 7 catches during the previous year (1976), and for catches from nearby pools in 1977 and 1978 (Figs 5b and 5c).

While there was an increase in the percentages of males of intermediate carapace lengths in Pool 3, the trend towards percentages below 50% was apparent for both large and smaller individuals (Fig. 4a). A scarcity of males over 30mm CL may therefore be typical of the Loddon River population during the study period; while the abundance of intermediate-sized males in Pool 3 may be aberrant. This contrasts with similar abundances of the sexes in smaller size classes in both Pool 3 and Pool 7 (Fig. 4).

Precocious males were also abundant in the small size classes, and the CL at which relative abundance of males decreased coincided exactly with the size range at which precocious males virtually disappeared from catches. Deviations from the 1:1 sex ratio among small *E. spinifer*, as well as the scarcity of large males, were considered due to the respective presence and absence of precocious males. Although smaller size classes were poorly represented in catches from other pools (Figs 5b and 5c) and precocious males were occasionally included in them, the long-term numerical contribution of the precocious group to *E. spinifer* populations remains unclear.

Skewed sex ratios in crayfishes are not unusual and Hogger (1988) reported that in some commercial catches only about 7% were females. That low proportion was considered due to seasonal migrations (from littoral to deep areas) but on the available data no estimates of natural mortality, emigration or recruitment in *E. spinifer* populations are possible.

Size Frequency Classes

Although catches in both Pool 3 and Pool 7 included high percentages of small individuals (Fig. 6), the size composition of catches was not stable over the period. Some of this variability was attributed to differences in average catchabilities at different carapace lengths. For example, the high percentage of the 30–40mm class from May-August 1978 (Fig. 6) would have been partly due to a higher catchability (~2x) that of other sizes

at this time (Table 2). However, as catchabilities were similar over most classes in each period and differences were not sustained in both periods, it is suggested that major catch composition changes are indicative of real trends in population size structure.

This skew towards smaller classes in Loddon River populations contrasts with *E. spinifer* catches taken in nearby catchments using the same techniques. Catches from the Georges River and Hacking River consisted entirely of larger individuals (50–110mm CL). Long-finned eels (*Anguilla reinhardtii*) were frequently observed at both these sites, while only two individual eels were sighted in the Loddon River over the entire study period. It is suggested that the high relative abundance of small crays at the study site may have reflected a low level of eel predation. Higher percentages of large adults have also been reported in a number of populations of three Victorian *Euastacus* (Barker 1992; Honan and Mitchell 1995a), but these values may reflect differing levels of harvesting or selection due to particular trapping techniques.

Increases in the relative numbers of small individuals (20–30mm CL) in Pools 3 and 7 from September-December 1977 (Fig. 6) are taken to represent recruitment of previously smaller crays into this size class. The majority of these individuals had recently moulted at the commencement of growth after winter (Turvey and Merrick 1997b), but this recruitment was neither preceded by, nor simultaneous with, catches of similar numbers of smaller individuals. Individuals in the 20–30mm size class dominated both populations early in the study. This domination was maintained into the 30–40mm class at the end of the study in Pool 3, and until August 1978 in Pool 7. A further pulse of recruitment into the 20–30mm size class may have commenced from September-December 1978 in Pool 3, but there was no evidence of this in Pool 7.

Assuming that catch frequency distributions reflected population size structures, and accepting that precocious males were capable of mating with mature females (Turvey and Merrick 1997a), relative abundances of mature females, precocious and normal mature males were estimated in the intact population of Pool 3. These estimations were designed to indicate the potential contributions of the two types of males to reproductive output. The true percentage for precocious males was probably higher than the calculated value (9%), as these individuals matured at less than 20mm CL and crays of this size were less catchable. The values calculated indicate that: only ~10% were adults (3% mature ♀, 6% normal mature ♂): there was a surplus of males; precocious males may have contributed significantly to successful mating. Furthermore, the large residual percentage of pre-reproductive individuals would suggest a high potential for population growth (Miller 1994).

Origins of the Precocious Group

Sexes becoming functional at different sizes is not unusual among crustaceans but this situation, of a significant proportion of the population comprising a third reproductive (precocious) group, has not been recorded for Australian crayfishes before.

It should be noted that in many areas where *E. spinifer* live, large individuals are sparsely distributed with the streams consisting of small and widely separated pools connected by shallow or ephemeral zones. So there are several potential benefits of developing this condition as a reproductive strategy, in an area with very limited habitat for large individuals. Firstly, the restricted suitable areas could be fully utilised by mature females. With minimal competition for limited resources from males mortality would be lowered and reproductive output maximised. Secondly, precocious males could successfully colonise shallows minimising direct competition with females. Thirdly, an ample supply of functional males would be available for a relatively small number of mature females, maximising successful spawning frequency.

Precocious males may be the result of the kinds of social interaction and inhibition now documented for *Macrobrachium rosenbergii* (Karplus et al. 1991, 1992); however, like other suggestions, relating to selection for male dimorphism (Gadgil 1972) and ran-

dom mortality of large males in small local populations (Ghiselin 1974), the idea of social control of growth was not tested and further discussion is not possible. It is also possible that the precocious male condition is triggered by short-term variability in the physico-chemical environment, but this is inconsistent with the apparent long-term stability of the upper Loddon habitat.

The authors have developed two hypotheses to explain the observed trends in abundance of males to female *E. spinifer*, but before discussing these, two general findings should be considered. Firstly, the reproductive studies (Turvey and Merrick 1997a) indicated that precocious males did not revert to the normal condition; while the reverse was unlikely at carapace lengths exceeding 20mm it may have occurred at smaller sizes. Secondly, it is possible that the high percentages of intermediate-sized males in Pool 3 were due to a chance aggregation.

The first hypothesis is that the decrease, in male abundance with increasing CL, resulted from the failure of initially abundant precocious males to attain a larger size. This also assumes that the relative abundances of females, precocious males and normal males from Pools 3 and 7 (Fig. 4) were typical of previous generations of crays in the study area. For this hypothesis to be acceptable, it is necessary to invoke some factor preventing most precocious males from attaining a size over 25–30mm CL. A cessation of growth alone is unlikely as, without high mortality, it would have resulted in an accumulation of precocious males at ~30mm CL and this was not indicated by the data. Furthermore, there was some evidence that growth rates of precocious males were similar to those of other individuals (Turvey and Merrick 1997b). If this hypothesis holds, then precocious males must have sustained almost 100% mortality over the 25–30mm CL range; this suggestion is supported by the dramatic decline in relative abundance of precocious males of this size in Pool 7 between May-August 1978 and September-December 1978 (Fig. 3).

The second hypothesis is that the increased abundance of males in smaller size ranges was due to a recent influx of precocious males that had not had time to attain a larger size. This implies: that during previous generations females were consistently more abundant than males at all sizes; that equal abundances of males and females in smaller classes during the mark-recapture study were due to the recent inclusion of numerous precocious males, in addition to normal males and at the expense of females. This hypothesis is supported by the increase in abundance of precocious males during the study in Pool 7 (Fig. 3), in association with a possible decrease in abundance of small females (Table 4 and Fig. 2) and by a lesser increase in the relative abundance of precocious males in Pool 3 (Fig. 3).

On the available data, it is impossible to exclude either hypothesis; they are not mutually exclusive when applied to data collected over a relatively short period.

Whilst the life cycle strategy of *E. spinifer* appears to be based on slow-growing large adults breeding for many years (Turvey and Merrick 1997a), the development of the precocious condition could be part of an alternative population survival strategy. In the event of severe environmental disruption and significant mortality of large adults the precocious individuals, in combination with newly maturing females, would potentially enable population numbers to be increased more quickly than if recruitment was based solely on output from slowly maturing adults of both sexes.

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